Flight Responses of Two Intertidal Gastropods

(Prosobranchia : Trochidae)

to Sympatric Predatory Gastropods from Barbados

BY

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INTRODUCTION

THE ROCKY INTERTIDAL ZONE of Barbados is exceedingly rich in species of gastropods. LEWIS (1960) records over 20 different species of prosobranchs inhabiting the narrow littoral zone. At the present time there is an inverse relationship between the number of species and the published reports concerning any aspects of their natural history and behavior. While in residence at the Bellairs Institute of McGill University on Barbados during January, 1977, we studied the escape responses of 2 species of top shells (Prosobranchia, Trochidae), *Tegula excavata* (Lamarck, 1822), the Green-based *Tegula*, and *Cittarium pica* (Linnaeus, 1758), the West Indian Top Shell. These herbivorous gastropods are ideal for studying escape behavior in that they are available in sufficient numbers and that they share their rocky habitat with at least 4 species of carnivorous gastropods (Prosobranchia, Thaididae): *Purpura patula* (Linnaeus, 1758), the wide-mouthed Purpura; *Thais haemastoma floridana* (Conrad, 1837), the Florida Rock Shell; *Thais rustica* (Lamarck, 1822), the Rustic Rock Shell; and *Thais deltoidea* (Lamarck, 1822), the Deltoid Rock Shell. Although temperate water species of top shells show well defined flight responses to asteroids (FEDER, 1963; YARNALL, 1964), the tropical top shells have been reported to show flight behavior to the presence of thaidid gastropods (CLARK, 1958). In a region of the Caribbean that is depauperate in predatory asteroids (LEWIS, *op. cit.*), the only carnivores that could be implicated as gastropod predators are the thaidids. Although the temperate species of *Thais* (now *Nucella*, ABBOTT, 1974) have been identified as predators of acorn barnacles (CONNELL, 1961, 1970), the number of acorn barnacles that were noted in the rocky intertidal zone of Barbados is extremely sparse and would preclude them from being a major food resource by the gastropods.

Through a study of the behavior of the 2 species of trochid gastropods presented with possible predators, we wish to demonstrate the flight responses and shed light on possible trophic relationships among this assemblage of intertidal gastropods.

DESCRIPTION OF SPECIES

Observations on all species of gastropods were made both in the field and in the laboratory during January, 1977. Field data were obtained and collections for laboratory experiments were made at 2 small indentations on the northeast exposed rocky coast of Barbados, River Bay (13°19′N; 59°36′W) and Little Bay (13°18′N; 59°35′W). In the laboratory the carnivorous species were kept separate from the herbivorous forms using 2 separate concrete holding tanks, both of which were supplied with running sea water, the temperature of which varied from 25.5 to 28° C during the period of the experiments. No attempt was made to provide any of the snails with food while in the laboratory, although the carnivorous forms were found to prey on each other.

The Herbivorous Gastropods

Tegula excavata is a common intertidal gastropod that ranges throughout the rocky shoreline of the Caribbean (ABBOTT, 1974). On Barbados the species is found in moderately large numbers under rocks and small boulders at the mean low water level, just in or below the "pink zone" of LEWIS (1960). There is little published information concerning the biology of this species. Approximately 150 specimens were collected at River Bay and ranged in shell axis length from 0.5 to 1.2 cm. From the size range for this species by WARMKE & ABBOTT (1962), both juvenile and adult specimens were used in our experiments.

Cittarium pica, an economically important species, ranges throughout the rocky intertidal zone of the Caribbean, but it appears only as fossils in Florida and Bermuda, although it apparently died out in these 2 areas in comparatively recent times (Clench & Abbott, 1943). Lewis (1960) reports that the juvenile stages occur in the "pink zone" above mean low water at Barbados. The adults are found from slightly above the water level to several decimeters below, usually within 60 cm of the surface (Randall, 1964). Many of the natives of Barbados supplement their diet with these large "whelks," often attaining diameters of over 10 cm. Almost all the adult animals that we were able to find were located in grooves and pits on the underside of large rocks and boulders below the mean water level at River Bay; whereas the juvenile animals were collected on the surface of exposed ledges at low tide in the "pink zone" above the mean low water mark at Little Bay. Approximately 100 specimens of *C. pica* were collected and ranged in shell axis length from 1.0 to 4.8 cm, mean length 1.9 ± 2.94 S. D.

The Carnivorous Gastropods

Purpura patula ranges in the Caribbean from Palm Beach, Florida south to Trinidad (Clench, 1947). Lewis states that the Barbados population is most abundant from mean sea level to a few decimeters above mean high water, regions Lewis has named the "black zone" and the "green zone." We have found many specimens of *P. patula* on the surface of exposed rocks as well as hidden in pits and depressions. Man appears to be the only real predator of this high intertidal gastropod, as many of the natives along the east coast collect them for food. According to Lewis (1960) the diet of *P. patula* consists primarily of the chiton *Acanthopleura granulata* (Gmelin, 1791) and the barnacle, *Tetraclita squamosa* Darwin, 1854.

Thais haemastoma floridana again has a rather broad distribution from North Carolina, south through the West Indies and along the Central American Coast to Trinidad (Clench, 1947). On Barbados, *Th. haemastoma floridana* is an open coast inhabitant found in the "pink zone" of Lewis from below mean low water to mean sea level. Many of the specimens that we collected had shell lengths in excess of 4.0 cm. Lewis (1960) again reports that "*T. floridana* is carnivorous and feeds upon barnacles, chitons and other molluscs."

Also found in the same "pink zone," but ranging below mean sea level, *Thais rustica* can be readily confused with the preceding species, although adults rarely exceed 3.0 cm in length (Abbott, 1974). At River Bay we observed many juvenile specimens between 0.4 and 1.2 cm below the mean low water mark in the surf zone of Lewis, beneath the algal canopy or among the clusters of the vermetid, *Spiroglyphus irregularis* (d'Orbigny, 1842). This species ranges from South Florida through the Caribbean south to the coast of Brazil (Clench, 1947). Lewis makes no mention of this species in his monograph, and little is known of its diet.

Thais deltoidea is found still further down in the rocky intertidal zone, generally below the low water level, although it does range upward to the lower portion of the "pink zone." Abbott (1974) reports that this species ranges from Jupiter Inlet, Florida, and Bermuda throughout the Caribbean southward to Brazil, and that it is "an abundant species where intertidal rocks are exposed to the ocean surf." At River Bay and Little Bay, most of the specimens of *Th. deltoidea* were quite large, shell length 3.0 to 4.5 cm, and heavily encrusted with coralline algae. Little is known of its feeding preferences.

EXPERIMENTAL METHODS

The following experiments were designed to test whether the 2 species of top shells would demonstrate escape responses to specific carnivorous gastropods, and to determine whether such behavior was induced by contact or distance chemoreception. Six to 10 specimens of either *Tegula excavata* or *Cittarium pica* were placed in glass finger bowls (top diameter 11.5 cm), each of which contained approximately 150 mL of sea water. The *T. excavata* ranged in shell length from 0.5 to 1.2 cm, whereas the *C. pica* were all juvenile animals with shell length varying from 1.0 to 2.6 cm (Randall, 1964). The experiments were designed to collect both descriptive and quantitative data by counting the number of top shells to leave the water in an arbitrarily determined time of 10 minutes after adding either the predator or an aliquot of sea water that contained the predator's "scent." In order to standardize the procedures the following steps were taken:
1) After being placed in the bowls, the snails were allowed to come to rest, usually 20 minutes before adding the carnivorous snails, 2) the experiments were performed between 0800 and 1100 Barbados time under the subdued lighting conditions of the laboratory, 3) an herbivorous gastropod, *Nerita versicolor* (Gmelin, 1791) was added to each of the control bowls in order to mimic the predator's presence by moving about the bowl acting as a potential disruptive agent, 4) to test for distance chemoreception, approximately 25 mL of sea water taken from a container that held one carnivorous snail per 100 mL of sea water was slowly added to a finger bowl that contained top shells.

The control for this experiment was adding an equal volume of sea water from the intake sea water valve to a

bowl with snails. When it appeared necessary, the data were tested for significance using the X^2 test for 2 independent samples (Siegel, 1956).

After some initial observations, it became apparent that there may be a differential size response of *Cittarium pica* to predatory gastropods. To test this hypothesis, the following experiment was performed: 6 small, juvenile *C. pica* (1.0 to 2.6 cm) and 6 large specimens (3.5 to 4.8 cm) were placed into each of four 2 L bowls that were half filled with sea water. After all locomotory activity had ceased in the bowls, usually 15 minutes, a specimen of *Thais deltoidea* (4.0 to 4.2 cm) was placed into each of 2 bowls, and a specimen of *Nerita versicolor* (3.0 to 3.5 cm) was added to each of the remaining 2 bowls as controls. The experiment was designed to measure the number of snails, and the size of these snails, to evacuate the bowls in 10 minutes.

RESULTS

1. Laboratory Experiments

Flight responses were elicited in *Tegula excavata* and *Cittarium pica* juveniles by 3 of 4 sympatric gastropod species that were tested in the laboratory (Table 1). A strong response was elicited when contact was made between the top shells and the carnivores. This was most apparent with *T. excavata*, for actual contact was not necessary to elicit a strong response in *C. pica*. The significance of contact to elicit a strong response in *T. excavata* can be seen in Table 1. The top shells that remain in the bowls, even after adding the carnivores, is almost half the total number. These top shells were not brought into direct contact with the carnivores, a case especially true for *Th. deltoidea* which is far less active than *Th. haemastoma floridana*. Generally the flight behaviors of both species were identical. The initial response was a slight elevation of the shell to expose the head, followed by a rapid flailing of the cephalic and epipodial tentacles. The top shells then exhibited increased locomotory activity, which usually resulted in the evacuation of the bowl of water. The behavior of *Te. excavata* differed from that of *C. pica* juveniles in that contact with such carnivorous species as *Th. haemastoma floridana* and *Th. deltoidea* often elicited a rapid, jerky torsion or twisting of the shell through an arc of 180°. This was most apparent when contact was made between the propodium of the carnivore and the soft parts or shell of the top shell. No such shell torsion or twisting was demonstrated by *C. pica* juveniles. On 3 separate occasions during the experiments, a specimen of

Table 1

	Size of Test Snail in cm	# of topshells in exptl. bowls at T_0	# to leave exptl. bowls in 10 min.	# topshells in control bowls at T_0	# to leave control bowls in 10 min.	Chi-Square Value
Tegula excavata	0.5-1.2					
Thais haemastoma floridana	3.0-4.2	75	62	75	0	—
Thais deltoidea	2.5-4.0	90	41	90	1	—
Thais rustica	2.0-3.0	40	21	40	1	—
Purpura patula	2.5-3.2	40	1	40	2	—
T. h. floridana water		32	5	32	0	3.471[1]
T. deltoidea water		32	11	32	2	6.178[1]
T. rustica water		32	8	32	1	4.655[1]
Cittarium pica (juveniles)	1.0-2.6					
Thais haemastoma floridana	3.0-4.2	40	36	40	0	—
Thais deltoidea	2.5-4.2	40	38	40	0	—
Thais rustica	2.0-3.0	24	16	24	0	—
Purpura patula	2.8-3.3	24	0	24	0	—
T. h. floridana water		40	35	40	0	—
T. deltoidea water		32	31	32	0	—
T. rustica water		24	3	24	1	—

[1]The difference between the experimental and control counts is significant ($p = 0.05$) when chi-square is greater than 3.840.

Te. excavata was captured, inverted and eaten by a specimen of *Th. haematoma floridana*. This occurred when the path to escape was blocked by other top shells in the bowl.

As well as exhibiting a strong response to contact, *Cittarium pica* juveniles react strongly to water that contained the "scent" of both *Thais haemastoma floridana* and *Th. deltoidea* (Table 1). When *Thais* water was added to a bowl of quiescent top shells, the snails became agitated and began to move about the bowls to the extent that most evacuated the bowls *en masse* within the first 3 minutes. On the other hand, *Tegula excavata* react less strongly to such water samples. Although there was tentacular flagellation, movement in the bowls tended to be slower and less direct. Even though a statistically significant number did vacate the bowls (Table 1), they did not do so simultaneously, and after 10 minutes those that did remain in the bowls had once more become quiescent.

There appeared to be a relationship between the age or size of *Cittarium pica* and its ability to respond to a predator (Table 2). Only the smaller, juvenile animals,

Table 2

Differential size response of *Cittarium pica* to *Thais deltoidea*

	Experimental Group	Control Group
Number of Large Topshells (3.5-4.8 cm) to vacate bowls in ten minutes or less (n = 12 per group)	0	0
Number of Small Topshells (1.0-2.6 cm) to vacate bowls in ten minutes or less (n = 12 per group)	11	0

with shell lengths between 1.0 and 2.6 cm, would respond to the presence of *Thais deltoidea*. The response was spectacular for in most cases the small top shells would evacuate the bowl not only within 3 minutes after adding the predator, but in unison. Although no motion was observed in the larger top shells with shell lengths between 3.5 and 4.8 cm, the cephalic tentacles did show slight flailing. When bowls that contained similar numbers and sizes of *C. pica* were moved out of doors in bright light or direct sunlight, all the top shells became highly agitated before the addition of the predator, although they would not evacuate the bowls.

2. Field Observations

During our residence on Barbados, field trips were made on a daily basis with one purpose being to observe possible feeding behavior of the carnivorous gastropods. Barbados is characterized by mixed semidiurnal tides. All observations were made during the lowest low tide sequence at either Little Bay or River Bay.

Purpura patula was observed feeding on 13 separate occasions on the striped nerite, *Nerita tessellata* (Gmelin, 1791). In all cases the carnivores were small specimens, averaging about 2.4 cm in length. The nerites had been flipped over and the purple shell was covering the ventral surface with its large foot. On 3 separate occasions we noted larger specimens of *P. patula* (average size, 4.0 cm) feeding on the chiton, *Acanthochiton granulata*. The chitons had also been flipped over and the purple shell had initially drilled (eaten) a hole through the center of the large foot to get at the viscera.

Thais haemastoma floridana and *Th. rustica* were not observed feeding in the field, although the former was a most opportunistic carnivore, even cannibal, in the laboratory holding tank. We did note a large number of *Tegula excavata* shells that were either empty or inhabited by small hermit crabs at River Bay. Generally we would find large specimens of both *Th. haemastoma floridana* and *Th. rustica*, in excess of 2.5 cm in association with *Te. excavata*. So they may be guilty of preying on them, guilty at least by association.

We did observe a *Thais deltoidea* (shell length 4.5 cm) in the process of consuming a carved star shell, *Astraea caelata* (Gmelin, 1791) with a shell length of 3.0 cm. We were unable to collect large numbers of star shells to test for flight behavior, but in 2 cases we did observe, under the laboratory conditions previously described, the shell twisting phenomenon when this species of star shell was presented to *Th. deltoidea*.

Although we did not make an actual count, we observed numerous large empty *Cittarium pica* shells scattered in the intertidal zone of River Bay. Many of these shells were broken at the apical end, exposing the dorsal visceral chamber. The only large carnivore besides man that was in evidence on the beach were the Sally Lightfoot crabs, *Grapsus grapsus*. Although they easily avoided capture and thus made direct measurements impossible, many of the males appeared to have carapace widths in excess of 15 cm.

DISCUSSION

Tegula excavata and juvenile *Cittarium pica* exhibit flight behavior that is typical of trochid gastropods (see Ansell, 1969 for a review). The differences between these 2 species appear to be in the sensory cues used to elicit the response, the complexity of the response, and most importantly, the age or size of the responding snail. The responses of *Tegula excavata* to carnivorous gastropods are mediated primarily through contact and in this regard differ from the responses of *C. pica* juveniles where predator detection appears to involve distance chemoreception. Clearly, there is an advantage conferred to a snail able to detect predators from a distance since contact with some carnivorous gastropods may be fatal; for example, contact with cone species where a toxin is injected by means of radular teeth in the eversible proboscis (Kohn, 1959). In the course of our experiments, we have observed that *T. excavata,* a snail that responds primarily to contact, was captured and eaten by *Thais haemastoma floridana* on 3 separate occasions, whereas under similar experimental conditions no *C. pica* were ever captured.

Shell twisting in *Tegula excavata* may be an additional adaptation to contact induced flight behavior as it would serve to extricate the top shell from the grasp of the prehensible foot of a carnivorous gastropod. Shell twisting was initially reported in Australian trochid gastropods, induced by thaidid snails (Clark, 1958). Apparently it is also quite commonly induced by molluscivorous echinoderms and gastropods in such genera as *Tegula* (Feder, 1963), *Gibbula* and, in addition to the more vigorous shell rolling movements, *Calliostoma* (Feder, 1967). The ability to twist the shell around the long axis of the visceral mass does cross familial boundaries in that we have observed it in the turbinids, *Astraea caelata* and *Turbo castanea* (Gmelin, 1791), although in this latter species, the response was elicited by handling and not by a specific predator.

The apparent dichotomy in response between adult and juvenile *Cittarium pica* is noteworthy. Differential size responsiveness has been reported only once. Montgomery (1967) reports that larger specimens of *Haliotis rufescens* Swainson, 1822 and *H. assimilis* Dall, 1878, are unresponsive to predatory asteroids, while smaller specimens exhibit shell twisting, mantle covering, and mucus expulsion. However, the possible significance of this phenomenon is not discussed.

Failure of the large specimens to respond can have several explanations, not mutually exclusive: 1) the larger snails may move into a zone unoccupied by predators, flight to which would confer an advantage; 2) the snails may attain a size relative to their predators at which they would be less susceptible to predatory tactics; 3) especially where contact is important, larger specimens may not receive stimulation sufficient to elicit a flight response; or 4) in a case where shell twisting is part of the flight repertoire, the shell may reach a bulk at which it would be energetically unfavorable to shell twist. In the case of *Cittarium pica*, the adults appear to migrate downward, entering a zone where different predators are encountered. Randall (1964) notes that one of the large top shells was found in the arms of a small octopus, and that octopods readily feed on live top shells. In addition, Randall has discovered top shells or their opercula in fish stomachs. Whatever the significance, we feel that it is important that future investigations address themselves to the possibility of size being a relatively important factor in the behavior of mollusks.

The 2 species of Barbadian trochids exhibit a strong response to those 3 species of *Thais* that share their habitat in the mid to lower intertidal zones. Although Randall (1964) observed a 3.5cm specimen of *Purpura patula* feeding on a 3.7cm specimen of *Cittarium pica*, neither species demonstrated a response to the presence or contact of *P. patula*, which from field observations appears to prey on other species of mollusks. *Purpura patula* is a high intertidal carnivore that may only on rare occasions be found in the lower zone inhabited by the 2 species of top shells. This situation may be similar to that of *Acmaea scabra* (Gould, 1846) which does not show an escape response to *Pisaster ochraceus*, with which it overlaps only at the lower extreme of its range in the intertidal zone, yet ranks high on a percentage basis of food for the asteroid (Feder, 1963). We feel that the relatively strong response of both *Tegula excavata* and juvenile *Cittarium pica* to *Thais haemastoma floridana*, *Th. deltoidea* and *Th. rustica* has ramifications in the predator-prey interactions of these species. Whether or not top shells comprise the major portion of the thaidids' diet and the extent to which the flight responses of potential prey are involved, remain unanswered until more ecological data are available.

SUMMARY

Two species of mid to lower intertidal top shells, *Tegula excavata* and *Cittarium pica*, exhibit flight behavior to the presence of 3 sympatric thaidid gastropods. The former species tends to respond strongly to contact with predatory

forms; whereas the latter primarily responds to distance chemoreception. Neither of the snail species responds to a high intertidal predatory gastropod, *Purpura patula.*

Also, there are 2 major differences in the behavior of the 2 top shell species in that only *Tegula excavata* shows the shell twisting response to contact and it is only the small or juvenile *Cittarium pica* that have a flight reaction to the predators, the adults being relatively unresponsive.

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